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SELENIUM AND PLANT: AN INVISIBLE BOND

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ABSTRACT

Selenium is a non-metallic element considered to be an essential nutrient for humans and animals. However, the effect of selenium on plants is controversial as it changes from beneficial to lethal over a range of concentrations. The food systems of few countries deliver an optimum level of selenium to their populations. Thus, knowledge of selenium uptake and metabolism in plants will help us to develop selenium enrich crop cultivars (biofortification) and also for plant mediated removal (phytoremediation) of excess selenium from soil and water.

KEYWORDS: Selenium, Plant System, Metabolism, Biofortification & Phytoremediation

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Original Article

1. INTRODUCTION

Selenium is a trace element belonging to the oxygen, sulphur family with some important functions in living organisms particularly in plants and animals. Selenium (Se) is an essential nutrient that is covalently bound in a number of different chemical forms found in plants. Selenium also plays an important role in various agricultural aspects. Selenium imposes myriad influences on DNA, causing stress, methylation, cell proliferation, apoptosis and has a major role to play in carcinogen metabolism, hormone production and immune function of a living system (Hatfield et al. 2014). Current interest in Selenium is focused on health benefits using plants with high Selenium contents as a source of cancer preventative Selenium compounds (Finley et al. 2001; Ip et al. 2002; Combs 2005). This review briefly summarizes selenium and its role, especially in plants, including selenium uptake, metabolism, and incorporation into proteins.

1.1 Biochemistry of Selenium

Selenium (Se) is a metalloid with the atomic number 34 and an atomic mass of 78.96. It is a member of the chalcogen family chemically related to sulphur and tellurium, elements in Group 16 (VIA) of the periodic table (Neal, 1995). It was discovered by Jons J. Berzelius in 1817.

In nature, Selenium exist in a number of inorganic forms like selenide, selenate, and selenite and organic forms like dimethyl selenide, selenomethionine, selenocysteine, and methylselenocysteine. Among the six naturally found isotopes of selenium, ^{74}Se, ^{76}Se, ^{77}Se, ^{78}Se, and ^{80}Se are stable (Zhu et al. 2014). Selenium is analogous to sulphur i.e both selenium (Se) and sulfur (S) is chemically similar. Since selenium is a chalcogen of sulphur, selenium is primarily dependent upon sulphate transporters for its uptake and metabolic activity in plants and other organisms (Mikkelsen et al. 1990). Se has been found to be hazardous at elevated levels because Se disrupts the function of molecules by replacing S in proteins and other compounds.

1.2 Selenium: In Environment

The presence of Se in the atmosphere is due to natural activities like soil erosion, volcanism and forest fires. Natural sources of selenium also include selenium-rich soils and selenium accumulator plants. Anthropogenic sources of selenium include burning fossil fuels and the mining and smelting of sulfide ores (Kabata-Pendias 1998). Human activities like and burning of garbage, tires and paper also increases the concentration of selenium in air (Mehdi et al. 2013). The senate is more bioavailable than Selenite in an alkaline environment and is comparatively less bioavailable in acidic conditions as it is more soluble and less adsorbed than silent, which is readily adsorbed to suspended solid particles (Chilimba et al. 2012).

The Selenium content mainly depends on its geographical distribution and usually ranges between 0.1 and 2.0 mg kg^{-1} in most soils (Dhillon and Dhillon 2003; Rodriguez et al. 2005). The concentration of selenium is less in surface waters than in ground waters due to minimal interactions between the rock surface and the water concerned. Freshwater predominantly contains selenate and selenite. On the contrary the surface water has a higher concentration of sodium selenate and selenide (Barceloux 1999).

1.3 Selenium: In Plants

1.3.1 Classification of Plants Based on Affinity for Selenium

The selenium concentration in plants depends on the chemical form of selenium, its concentration and bioavailability in soil and the accumulation capacity of the plants (Zhu et al. 2009). The availability of soil Se to crops also depends upon irrigation, aeration, liming and selenium fertilization (Gissel-Nielsen 1998). Plants grown on seleniferous soil can be broadly categorized as primary or secondary indicators/accumulators and non-accumulators based on the influence of selenium on them (**Table 1**) and concomitantly their physiological response which varied with the plant species. Terry et al. (2000) classified plants as Se tolerant i.e Se accumulators (plants accumulate very high concentrations of Se e.g. members of *Cruciferea*) and Se sensitive or non-accumulators (plants are susceptible to selenium accumulation). The accumulator plants supposedly did not have any specific pathways for selenium uptake. These plants simply metabolized Se and S indiscriminately at elevated rates compared to non-accumulators. Another category of plant species (belonging to the families Brassicaceae, Fabaceae, and Asteraceae) called Se hyperaccumulators are able to accumulate Se to levels 100-fold higher than the surrounding vegetation in a particular field. These Se hyperaccumulators can distinguish between S and Se and have Se-specific metabolism. Apart from above, few species of plants like *Astragalus* species (including some locoweeds), prince's plume (*Stanleya* sp.), asters (*Xylorhiza* sp.), and false goldenweed (*Oonopsis* sp.) are also known as Selenium indicators because such plants can flourish only on soil with a high content of selenium. Plants like *Aster, Atriplex, Gutierrezia* has reportedly accumulated Selenium in moderate but toxic concentrations (William et al. 2003).

Table 1: Summary of Plants that Accumulates Selenium

Group	Type	Name of plant	Amount of Se accumulated	Reference
I (Primary Indicators)	Accumulator	Garlic (Allium sativum L.), onion (Allium cepa L.), brocolli (Brassica oleracea L.) and wild leek (Allium tricoccum L.)	Hundreds to several thousand mg Se kg-1 dry weight	Whanger 2002 Roberge et al. 2003
	Hyperaccumulators	Astragalus sp, Stanleya sp, Morinda sp, Oonopsis sp. and Xylorhiza sp.	Hundreds to several thousand mg Se kg-1 dry weight	Dhillon and Dhillon 2003; Ellis and Salt 2003 Freeman et al. 2006b.
II (Secondary Indicators)		Indian mustard (Brassica juncea) and canola (Brassica napus) and some species of Astragalus, Atriplex, Castilleja, Comandra, Grayia, Grindelia, Machaeranthera and Mentzelia	Accumulates modest amounts up to 1000 mg Se kg-1 dry weight.	White 2015
III (Non-Accumulators)		grains, grasses, most forage and crop plants (Rice Wheat, Maize,Potato)	Accumulates less than 25 mg Se kg^{-1} dry weight usually; maintains a ceiling of 100 mg Se kg^{-1} dry weight	White et al. 2004, Rani et al. 2005

1.3.2 Uptake, Assimilation and Metabolism of Se in Plants

In higher plants, metabolism of Selenium (Se) is closely related to that of Sulfur (S) due to their chemical similarity (Shibagaki et al. 2002; El Kassis et al. 2007). Since Se and S are chalcogens, the presence of S acts as a limiting factor during uptake of Se as they both compete for the same transporters (White et al. 2007). It has been established through sequence analysis that the sulphate transporter includes 12 membrane-spanning domains. The sulphate transporter can be broadly categorized into two main classes based on its affinity to Sulphate. The high-affinity transporter or supposedly the primary transporter is regulated by the sulphur concentration in the plant tissue. It is expressed mainly in the roots and has a *K*m for sulfate of 7-10 µM. The low-affinity transporter expressed in both roots and shoots has a higher *K*m for sulfate of 100 µM. It is assumed that the low affinity transporter has a role to play during the intercellular transport of sulphate from apoplast into symplast (Takahashi et al. 2012). The hyperaccumulators of selenium absorb more Se than S whereas the non-accumulators shows selective uptake of selenate compared to sulphate (White et al. 2004). Selenate is more soluble and available for plants than selenite under oxidizing and alkaline soil conditions (Mayland., 1991; Chilimba et al. 2012;Kikkert and Berkelaar 2013) Selenate is actively translocated from the roots into the shoots of the concerned plant with the help of sulphate transporters and its respective assimilation enzymes (White et al. 2004; Gigolashvili and Kopriva 2014).

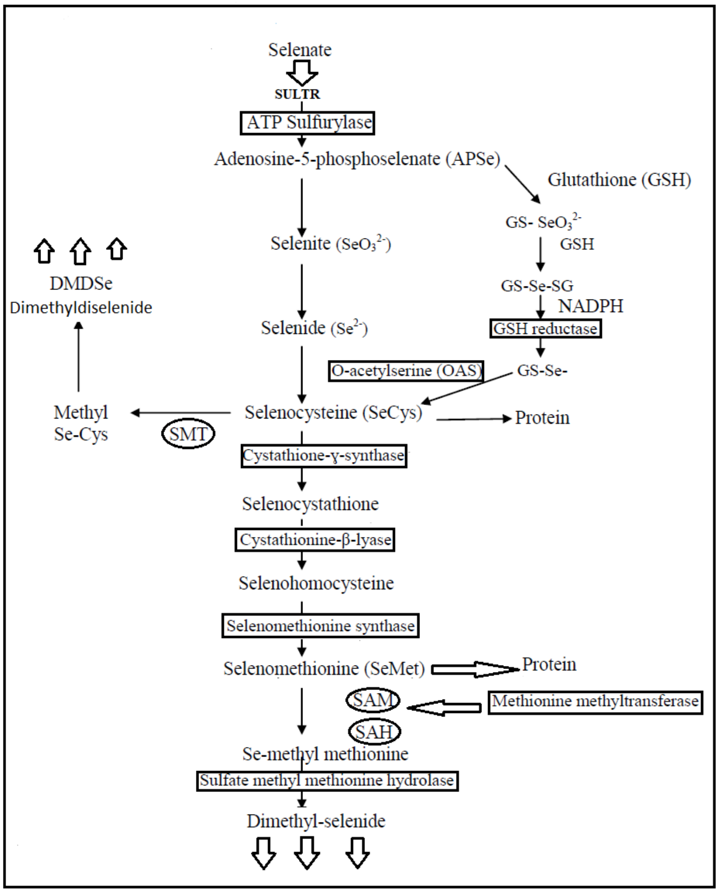

Figure 1: Schematic Overview of Se Metabolism in Plants (Adapted from Malagoli et al. 2015)

(SMT: Selenocysteine methyl transferase; SAM: S-adenosylmethionine; SAH: S-adenosyl homocysteine; GS-SeO_3^{2-}: Seleniteglutathione; GS-Se-SG: Selenodiglutathione)

Selenate assimilation takes place predominantly in the leaf chloroplasts (Pilon-Smits et al., 2010). Selenate is reduced to selenite in a rate-limiting step with the help of two enzymes i.e ATP sulfurylase (APS) which couples selenate to ATP, forming adenosine phosphoelenate (APSe) followed by APS reductase (APR) which further helps to reduce selenium to selenite (Wilson and Bandurski., 1958; Murrillo and Leustek, 1995). Isozymes for APS and APR exist in both chloroplast and cytosol, but most of the selenate reduction supposedly occurs in the chloroplast. Selenite is further reduced to selenide in the chloroplast with the help of sulfite reductase. Contrarily nonenzymatic reduction by reduced glutathione (GSH) also has a significant role to play in the selenite reduction (Anderson 1993; Terry et al. 2000). Selenite reacts nonenzymatically with GSH to form selenodiglutathione (GS-Se-SG), an intermediate compound. Selenodiglutathione is further reduced to selenol (GS-SeH) and then to selenide (GS-Se) with the help of enzyme GSH reductase (Ng and Anderson., 1978). The reduction of GS-Se-SG to selenol (GS-SeH) may also occur non-enzymatically (Anderson and Scarf., 1993). Subsequently selenide is coupled to O-acetylserine (OAS) to form SeCys with the help of OAS thiol lyase (also called cysteine synthase) in the cytosol, chloroplasts, and mitochondria. OAS is synthesized by the enzyme serine acetyl transferase. It primarily functions as a signal molecule to induce the activity of sulfate transporters and sulfate assimilation enzymes during Se metabolism in plants (**Figure 1**). Se is ultimately incorporated into seleno proteins forming the unique amino acids SeCys and SeMe. Addition of a methyl group to SeCys by a specific transferase results in the

formation of SeMSC (Neuhierl and Bock 2000; Pickering et al. 2003). According to Pilon-Smits et al. (2010) SeCys may be converted to SeMet with the help of three enzymes namely cystathionine-g-synthase (CgS), cystathionine-b-lyase and Met synthase or it can be converted to elemental Se (Se) by the activity of a selenocysteine lyase (SL) found in both chloroplasts and mitochondria (Mihara and Esaki., 2002). SeCys forms methyl- SeCys with the help of SeCys methyltransferase (SMT). The pronounced activity of SeCys methyltransferase (SMT) in hyperaccumulators, suggests that these species accumulate Se predominantly in the form of methyl-SeCys, while most other species accumulate selenium as selenate (de Souza et al. 1998; Freeman et al. 2006b). Methyl-SeCys is further converted into the predominant volatile form of Se dimethyldiselenide (DMDSe) in Se hyperaccumulators (Terry et al. 2000; Kubachka et al.2007; Sabbagh and Van Hoewyk 2012). Selenoadenosylmethionine (SAM) plays a significant role as a methyl donor during transformation of selenite or seleno methionine (SeMe) or methyl selenocystine (methyl-SeCys) to DMSe and DMDSe respectively (Ranjard et al., 2002).

2. SELENIUM: SIGNIFICANCE IN PLANTS

Although lower group of plants such as algae require Se for growth (Lindstrom. 1983), it is not considered to be an essential nutrient for higher plants (Terry et al. 2000). Numerous studies have shown that at low concentration selenium exerts beneficial effect on growth and stress tolerance (Hartikainen 2005; Dianaguiraman et al. 2005; Das et al.2011). Selenium also affect several important physiological and biochemical processes in plant species (Pennanen et al., 2002; Das 2018). Selenium can regulate some ions absorption e.g. phosphorus and also increase plant resistance against oxidative stress caused by production of free radicals (Hartikainen et al., 2005). Selenium accumulating plants limit the integration of selenoamino acids into proteins by converting selenium into soluble non protein selenoamino acids like Se methylselenocysteine and selenocystathionine (Terry et al. 2000; Wanger. 2002; Rayman et al. 2008). Se-methylselenocysteine in particular exhibits chemoprotective effects against cancer (Finley et al. 2004). Accumulators of MetSeCys would be particularly useful for the production of fortified crops, since this form of Se is anticarcinogenic (Unni et al. 2005).

As described above, all plants can take up inorganic selenate and selenite and assimilate them to SeCys and other organic selenocompounds, including volatile forms. To further enhance plant Se accumulation, tolerance, and volatilization, various transgenic approaches have been used (Nyberg 1991; Ellis et al. 2004; Pilon-Smits and LeDuc 2009). These properties of plants may be utilised efficiently to remove excess levels of Se (Pilon-Smits 2005; Bañuelos et al. 2010) in the environment (phytoremediation), and also produce fortified foods (Lin et al. 2014) to prevent Se deficiency (biofortification). In Se-polluted environments methylation of inorganic Se oxyanions to volatile species offers an alternative approach to bioremediation of selenium compounds. The bioavailability of Selenium to crop plants as a source of micronutrient depends on the oxidation of reduced selenium species. In an engineered aquatic ecosystem designed for brine shrimp production, it was observed that microalgae, bacteria, and diatoms were able to cause various metabolic biotransformations of selenate to organic selenium compounds like selenite to selenide including elemental form of Selenium. These selenium enriched invertebrates produced as a result of biological metabolic transformations and/or phytoremediation may be effectively introduced into the food chain for human and animal consumption (Schmidt, 2013).

3. CONCLUSIONS

Excess selenium in the atmosphere becomes hazardous to the existence of both aquatic and terrestrial organisms. Although it is a known environmental pollutant, selenium is also considered as an invaluable, rare metalloid and an essential micronutrient. Selenium is ubiquitous in soils, but exists mainly in insoluble forms. Hence Se is often of limited availability to plants. Consequently, it is often supplied by plants to animals and human consumers at levels too low for optimum health. The invisible bond between plant and selenium as well as its uptake and metabolism via sulphate transporters can thus be exploited to develop affordable biofortified crop cultivars with adequate selenium content in order to fulfil the requirement of this important element to all strata of mankind.

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